A PHYLOGENETIC ANALYSIS AND REVISED CLASSIFICATION OF THE NORTH AMERICAN HAPLOTREMATIDAE (GASTROPODA: PULMONATA)

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ABSTRACT

A revised classification of the North American Haplotrematidae (=Haplotrematinae) is presented, based on character compatibility analysis of 25 characters of the musculature, reproductive system, radula, kidney, pericardium, and shell. Two genera are recognized -- Ancotrema and Haplotrema, the latter with three subgenera, Ancomena, Geomene, and Haplotrema, sensu stricto. The hypothesized age of the Haplotrematinae is 42.5 million yr (late middle Eocene), when the temperate Haplotrematinae and its tropical out-group, the Austroselenitinae, are assumed to have diverged. The phylogenetic hypothesis indicates an early dichotomy between Ancotrema and Haplotrema, with the species of Ancotrema retaining more characteristics of the hypothetical ancestor. Other evolutionary trends include: (a) a tendency toward reduction of vaginal musculature; (b) a parallel tendency toward greater penial complexity; (c) migration of the origin of the penial retractor muscles from the columellar muscle bundle to the floor of the lung (presumably increasing mechanical efficiency); (d) parallel instances of gigantism in the Pacific Northwest; (e) size reduction southward along the Pacific Coast, correlating with the presence/severity of a summer dry season; (f) a homoplastic continuation of the loss or reduction of cusps on the teeth of the radula. A lectotype is designated for Selenites vancouverensis forma hybrida Ancey, 1888.

The Haplotrematidae are a specialized family of rhytidoidean land snails restricted to the Western Hemisphere. Baker (1941) divided the family into the subfamilies Haplotrematinae (North American) and Austroselenitinae (Antillean and South American). The Haplotrematinae constitute a holophyletic group (sensu Ashlock, 1971), based on characters of the kidney, ureter, sigmoid loops of the hindgut, salivary gland conformation, jaw, and radula. In the current classification (Pilsbry, 1946), which draws heavily on the detailed anatomical studies of Baker (1931, 1941), all species of Haplotrematinae are assigned to the genus Haplotrema Ancey, 1881. [The classification of Zilch (1960) merely strews all previously proposed genera and subgenera of Haplotrematidae as subgenera under the genus Haplotrema.] Table 1 compares the classifications of Baker (1931) and Pilsbry (1946), both of which used the non-standard category "section," with the classification proposed in this paper.

Since the time of those authors' writings, methods have been developed that enable systematists to analyze patterns of character variation in accordance with stated criteria in order to develop hypotheses about the evolutionary history of groups of organisms. The purpose of this study is to apply some of these methods to derive a classification of the species of Haplotrematinae that is supported by as many independent characters as possible and therefore represents the best available estimate of the phylogenetic relationships of these taxa. The method used is character compatibility analysis (Estabrook, 1972; Le Quesne, 1982), which has its roots in the observations of Wilson (1965) and Le Quesne (1969, 1972). Character compatibility analysis is the method of choice where, as here, one seeks the tree exhibiting the most congruence in the synapomorphy pattern of the taxa under study (Strauch, 1984). The analysis incidentally provides a test of how well the characters studied and utilized by Baker (1931, 1941) support his own classification.

This inquiry grew out of my preparation of: (a) a treatment of the Haplotrematidae for the Council of Systematic Malacologists "Checklist of the Non-marine Mollusca of the United States and Canada" (Pratt, in prep.) and (b) an identification manual of the land snails and slugs of California for the California Departments of Food and Agriculture and Fish and Game. This analysis and discussion are beyond the scope of either of those works, and so are presented in this paper.

Table 1. Comparison of classifications of the North American Haplotrematidae (=Haplotrematinae).

Baker (1931)	Pilsbry (1946)	This Paper
Genus *Haplotrema* Ancey, 1881	Genus *Haplotrema*	Genus *Haplotrema*
subg. *(Haplotrema, s.s.)*	subg. *(Haplotrema, s.s.)*	subg. *(Haplotrema, s.s.)*
sect. *Haplotrema, s.s.*	sect. *Haplotrema, s.s.*	subg. *(Geomene)*
sect. *Geomene* Pilsbry, 1927	sect. *Geomene*	subg. *(Ancomena)*
subg. *(Ancotrema)* Baker, 1931	subg. *(Ancomena)*	Genus *Ancotrema*
sect. *Ancotrema, s.s.*	sect. *Ancomena, s.s.*	
sect. *Ancomena* Baker, 1931	sect. *Greggiella* Baker, 1941	
	sect. *Ancotrema*	

MATERIALS AND METHODS

Character compatibility analysis (Estabrook, 1972, 1978) was used to identify patterns of agreement and disagreement among characters in the data set and to identify which characters were most useful in constructing an estimate of the phylogenetic relationships among the 16 valid specific and infraspecific taxa assigned to the Haplotrematinae. This analysis was performed manually according to the method described by Meacham (1981), and subsequently using the Fortran program CLINCH by Kent L. Fiala, with identical results. Examples of the use of character compatibility analysis include Duncan (1980) and Meacham (1980), where further references to its theoretical and mathematical basis can be found.

The basic structure of the phylogenetic hypothesis was established from the primary clique(s) of characters derived through compatibility analysis. Then rejected characters and character state trees were re-evaluated for the additional information they could provide.

Anatomical data are lacking for some of the taxa of the Haplotrematinae. Four taxa regarded by previous authors as species either have not been dissected or the available anatomical information is incomplete. They are therefore excluded from the analysis: tentative suggestions for their placement are given in the discussion. The subspecific relationship between *Haplotrema duranti duranti* (Newcomb, 1864) and *H. d. contintentis* (Baker, 1931) is maintained, although only shell and radular data are available from *H. d. duranti*. One other taxon is regarded as a *species inquirenda*.

Sources of data are listed below. The abbreviations BR and TP designate locality numbers from the collections of the author (San Francisco, California) and of Timothy A. Pearce (Ann Arbor, Michigan), respectively. In addition to the anatomical material cited, approximately 900 lots of shells were examined, mainly in the Santa Barbara Museum of Natural History, California Academy of Sciences, and the author's collection.

TAXA INCLUDED AND DATA SOURCES

alameda Pilsbry, 1930. Baker (1931); author's dissection of nominal subsp. *fieldi* Pilsbry, 1930, from Kern River canyon, 1.6 km southwest of Democrat Hot Springs, Kern County, California (BR 957).

caelatum (Mazÿck, 1886). Baker (1931, 1941).

concavum (Say, 1821). Baker (1931), Pilsbry (1946);

additional information on genitalia from Webb (1943). Subsp. *minus* (Ancey, 1882) is a synonym (Pilsbry, 1946).

duranti (Newcomb, 1864). Radula from topotypic subsp. *duranti* (Baker, 1931); other anatomy based on *H. d. continentis* Baker, 1931 (Baker, 1931).

hybridum (Ancey, 1888). Baker (1931); author's dissection from Cape Blanco, Curry County, Oregon (BR 1173). Figure of genitalia by Webb (1961) shows some characters as in *Ancotrema sportella*, others equivocal [e.g. bulge on left side of vagina labeled "pilaster" resembles muscular collar found in this position in *A. sportella* (Gould, 1846) and other species]. Although Baker (1931) reported intergradation between "the *semidecussatum* form of *hybridum*" and *A. sportella* in western Washington, in northwest California and southwest Oregon *hybridum* occurs at the same localities as typical *A. sportella* and *Haplotrema vancouverense* (Lea, 1839) without intergradation. Lectotype designation in a following section fixes type locality as Astoria, Oregon.

"Form" *semidecussatum* Gratacap is not an available name. The original publication (as *Macrocyclis vancouverensis* [Lea] var. *semi-decussata*) was not intended as the proposal of a new taxon but merely the reference to a museum label (apparently from Thomas Bland) accompanying "a very interesting specimen...from Astoria, Oregon" (Gratacap, 1901:340). The text goes on to quote the opinion of H. A. Pilsbry that "it should not be accorded position and is probably var. *hybrida* Ancey" (Gratacap, *loc. cit.*). Baker (1931) provided diagnostic information but treated it as infrasubspecific "form" of *"Haplotrema sportella hybridum."* The anatomy is reported to be the same as in *A. hybridum* (Baker, 1931).

"Var." *depressa* Ancey, 1888, is an unavailable infrasubspecific name.

keepi (Hemphill, 1890). Baker (1931); Webb's (1961) figure of genitalia of specimen from Dog Creek, Shasta County, California, and author's dissection from Signal Butte, Shasta County (TP 861026-1215), differ in characters of the penis and spermathecal duct and could represent a different, undescribed species.

minimum (Ancey, 1888). Baker (1931); author's dissections from Duncan Point, Sonoma County (BR 1466); Point Reyes Peninsula, Marin County (BR 1490, BR 1640, BR 1642); San Pablo Dam Road above San Pablo Reservoir, Contra Costa County (BR 316); Sharps Park, San Mateo County (BR 104); Malpaso Creek, Monterey County (BR 1503), California. "Forms" *occidentale* (Hemphill *In:* W. G. Binney, 1892),

tenue (Hemphill *In:* W. G. Binney, 1892), and *kelseyi* (Hemphill, 1911) are synonyms (Pilsbry, 1946).

sportella (Gould, 1846). Baker (1931); author's dissections from along Woods Creek, west of Philomath, Benton County, Oregon (BR 1681); Moonstone Beach, Humboldt County, California (TP 831228-1). Figures of genitalia by Webb (1961) corroborate some characters. Porter's (1965, 1968) figures of the genitalia of a specimen from near Corvallis, Oregon, show an extremely short, saccular spermathecal duct with a pointed end, not otherwise reported in the species. A specimen that I dissected from Woods Creek, about 15 km west of Corvallis (BR 1681), has the elongate spermathecal duct and globose spermatheca normal in the species. Perhaps Porter's (1965, 1968) material was abnormal, or the structures were misinterpreted.

transfuga (Hemphill *In:* W. G. Binney, 1892). Baker (1941).

vancouverense (Lea, 1839). Baker (1931); author's dissections from Brookings, Curry County, Oregon (BR 357); Luffenholtz Beach, south of Trinidad, Humboldt County, California (BR 354). Figures of genitalia by Webb (1961) and Porter (1965, 1968) add no new information. "Forms" *vellicatum* (Forbes, 1850) and *chocolatum* (Dall, 1905) are synonyms (Pilsbry, 1946), although a lectotype designation for *chocolatum* may be needed to confirm this (cf. remarks by Henderson 1936:257).

voyanum (Newcomb, 1865). Baker (1931, 1941); author's dissection from Bidden Creek, Trinity County, California (BR 1229).

TAXA NOT INCLUDED IN THE ANALYSIS

catalinense (Hemphill *In:* W. G. Binney, 1890). Not dissected.

costatum Smith, 1957. Not dissected.

guadalupense Pilsbry, 1927. Not dissected.

humboldtense Pilsbry, 1946. Based on material that Baker (1931) included in *H. voyanum*, *Haplotrema voyanum humboldtense* Pilsbry, 1946, was described in such vague terms and with such a generalized type locality ("Humboldt and 'Klamath' counties," Calif.) that even a meaningful search for the type population would be difficult. Whether Klamath County, Oregon, was meant (Baker, 1931:421) or the former California county of the same name, as in Pilsbry's interpretation, is not known. Until such time as the type material can be matched up with a population somewhere, *H. v. humboldtense* must remain a *species inquirenda*.

kendeighi Webb, 1951. Originally described as a subspecies of *Haplotrema concavum*; regarded as a species by Hubricht (1956, 1985). Dissection by Hubricht (1956) incompletely described.

CHARACTERS

Appendix A lists the characters, character states, and hypothesized character state trees used in the analysis. Characters of the musculature, reproductive system, radula, kidney, pericardium, and shell are included. No weighting was assigned *a priori* to the characters of any one system.

The polarity of character state transformations was inferred mainly on the basis of out-group comparison at various levels of generality, and in some cases by correlation of equivocal characters with the direction of other, better-grounded transformations. For example, the reduction of radular tooth secondary cusps (apomorphous states of characters 3-5) parallels a well-established, general trend in carnivorous land snails and slugs toward a "slicing" or "stabbing" tooth morphology (Watson, 1915; Solem, 1974). Some use was made of the assumption that the most common state of a character is primitive. The Haplotrematidae have no significant fossil record, so no inferences could be based on stratigraphic precedence.

Direction of "chorological progression" — suggested by Hennig (1966) as one method of inferring polarity — could be based, for example, on the observation that the Klamath Mountains are a refugium preserving vegetation (Whittaker, 1961; Axelrod, 1976) and perhaps a land snail fauna (Roth, 1981) more like that of the later Cenozoic than any other region in the west. This would lead to the hypothesis that character states found in *Haplotrema voyanum* and *H. keepi*, residents of the Klamath region, are primitive within their clades. However, one of the uses of a phylogenetic hypothesis is to illuminate the biogeographic history of a group, and excessive reliance on this form of reasoning would introduce circularity into a biogeographic analysis. Chorological progression therefore was considered only in the spirit of "reciprocal illumination" (Hennig, 1966; Page, 1987).

Table 2 shows the distribution of character states among the 12 taxa included in the analysis. A hypothetical ancestor, with all characters in the inferred primitive condition, is added. Its character states are not necessarily those of the Austroselenitinae, because the species of that tropical group have specializations of their own [for example, the slender, elongate atrium of *Austroselenites (Zophos) concolor* (Férussac, 1820) (Baker, 1941:pl. 9, fig. 6)]. Comments on specific characters follow.

The right ocular retractor is free from the genitalia (character 1, state B) in all Austroselenitinae dissected (Baker, 1931, 1941). Posterior position of the external genital orifice (character 2, state B) is an apomorphy of the Haplotrematinae (and perhaps Haplotrematidae) in general, but plesiomorphous within the group. *Haplotrema* generally enter the shell of a prey snail through the aperture or through a hole broken just behind the peristome (pers. observ.); relocation of the genital apparatus backward probably allows the head and foreparts to reach farther inside the shell. A genital orifice close to the base of the right ommatophore (characters 2, state A) in *Haplotrema duranti* and *H. caelatum* probably represents a space-related reversal in these small-sized species. On Santa Barbara Island, California, *H. duranti* preys on the pupillid snail *Nearctula rowelli* (Newcomb, 1860), entering the shell through the side of the whorls of the spire (F. G. Hochberg, pers. comm., 1979); it probably does not require the extreme elongation of the foreparts needed by species that go up the body whorl of their prey.

Character 4 (multiple/reduced number of cusps on central tooth of radula) is kept separate from character 5

Table 2. Distribution of character states among species of North American Haplotrematidae and hypothetical ancestor.

Taxon	Symbol	Character No.				
		1-5	6-10	11-15	16-20	21-25
caelatum	CAE	AABBB	CAABA	AABAA	ACBAB	BAABB
concavum	CON	ABABA	CAABA	BABBB	ACBAB	BBDBA
duranti	DUR	AAABA	CAABB	BABBB	ACBAA	ABCBB
hybridum	HYB	BBAAA	AAABB	AAABB	BAABC	ABAAA
keepi	KEE	BBABA	CAAAB	CABBB	BCBCA	ABDBA
minimum	MIN	BBABA	CABBB	AABBB	BABAA	ABDBA
alameda	ALA	BBABA	CAABB	BABAB	ABBAA	ABBBB
sportella	SPO	BBAAA	AAABB	AAABB	BAABC	ABAAB
transfuga	TRA	BBABB	CAABB	BABAB	ABBAA	ABBBA
vancouverense	VAN	BBABA	CBBBB	ABBBB	BACAA	ABDBA
voyanum	VOY	BBAAA	BAABB	AAABB	BABAC	ABAAB
ancestor	ANC	BBAAA	AAABB	AAABB	BAAAC	ABAAA

(presence/absence of cusps on central tooth) because multiple cusps could be lost without passing through a stage of reduction in number. Migration of the origin of the penial retractor muscle from the columellar bundle to the floor of the lung (character 6) probably represents a transition toward greater mechanical efficiency. A tendency for the main penial chamber to be differentiated into apical and basal parts (character 13) is also seen in the out-group Austroselenitinae.

RESULTS

PRIMARY CLIQUES

Two primary cliques of 17 characters each were derived. The cladograms based on these cliques are shown in figure 1. Symbolic abbreviations of species names used in the figures and in the following discussion are given in Table 2. Characters 3, 7, 8, 9, 12, 15, and 22 are compatible with all others in the analysis (all but character 8 are characters unique to one analyzed species) and are therefore common

to both primary cliques. In addition to these "consensus" characters, both cliques include characters 1, 4, 6, 10, 13, 18, 19, 21, and 24. The two cliques differ only in the presence of character 16 (clique A) or character 17 (clique B). The components of cladograms A and B grouping (ANC,((SPO,HYB), VOY)) and (DUR,(CON,CAE)) are isomorphous in both cladograms. The cladogram based on clique A, with character 16 (atrium with/without stimulator), contains an unresolved trichotomy. The cladogram based on clique B, with the multistate character 17 (vagina with shining muscular collar/with sphincteric thickening/without collar or thickening), is more fully resolved and is accepted as the best estimate of actual patterns of ancestry and descent in the Haplotrematinae.

OTHER CHARACTERS

2. An external genital orifice close to the right ommatophore in DUR and CAE is a probable homoplasy associated with small size.

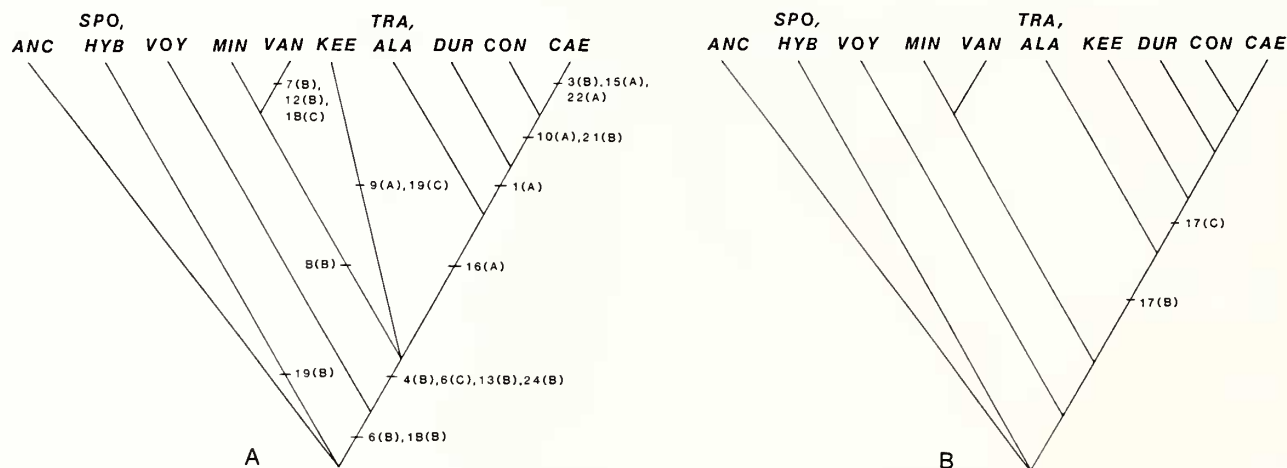5. Absence of cusps on the central tooth of the radula

Fig. 1. Cladograms based on the two primary cliques: (A) based on clique with character 16; (B) based on clique with character 17. Abbreviations of taxa as in Table 2. Numbers on branch segments designate apomorphic states of characters as defined in Appendix (shown in B only where different than in A).
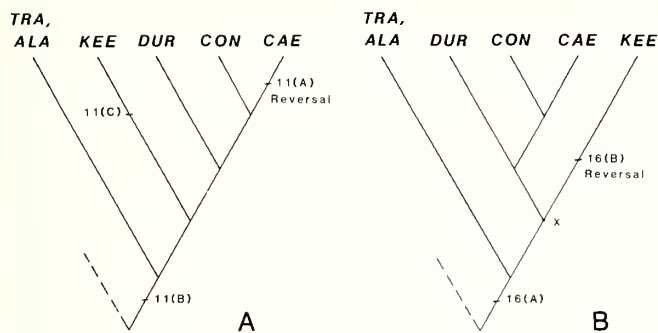
Fig. 2. The right-hand branch of cladogram B (from Fig. 1) with inferred apomorphies and reversals of character 11 (A) and character 16 (B). Component (KEE,(DUR,(CON,CAE))) is rotated around node x in right diagram for clarity; the order of branching remains unchanged.

is a homoplasy, occurring independently in TRA and CAE.

11. Sharp papillae are present on the penial wall of (TRA,ALA), DUR, and CON; blunt papillae are present in KEE. As shown in figure 2, derivation of blunt papillae from sharp, and one reversal (to papillae absent in CAE), are sufficient to incorporate this character into the basic cladogram.

14. A penial sheath is present in CAE and (TRA,ALA); homoplastic origins are indicated.

16. A stimulator is present in the atrium in (TRA,ALA) and (DUR,(CON,CAE)) but absent in KEE. As shown in figure 2, a single reversal is sufficient to incorporate this character into the basic cladogram.

20. The relative length of the kidney is greatest in ((MIN,VAN),((TRA,ALA),KEE,DUR)) and least in ((SPO,HYB), VOY); a partial reversal involving (CON,CAE) is indicated. When recoded C → A → B, this character becomes compatible with the primary clique.

23. A basic trend from broad to narrow radial ribs is established but the absence of ribs is homoplastic. Unribbed shells apparently have been derived from shells with broad, narrow, or threadlike ribs. The presence of broad ribs in CAE represents at least a two-step reversal.

25. Minute, wavy spiral striation may be generally distributed through the Haplotrematinae but its expression masked on ribbed shells. Its distribution in the group studied approximately parallels that of smooth shells, which is homoplastic.

DISCUSSION

Figure 3 presents the hypothesis of the phylogeny of the Haplotrematinae produced by this study. Five characters from five systems (radula, musculature, kidney, reproductive system, and shell) support the dichotomy between the group (ANC,((SPO,HYB),VOY)) and the rest of the subfamily. The former group consists of the species that Baker (1931) referred to the nominate "section" of Ancotrema. Neither primary clique contains an apomorphy defining Ancotrema or distinguishing it from the hypothetical ancestor; the group is paraphyletic. A plausible alternative coding of character 24,

with state A (coarse spiral striae cutting tops of radial ribbing) as apomorphous, would distinguish Ancotrema but is not compatible with characters 6 and 18. Similarly, round-topped radial ribs wider than their interspaces could be apomorphous in Ancotrema.

An alternative, less parsimonious interpretation, which would allow VOY to be grouped with (SPO,HYB) on the basis of these shell characters, is that migration of the penial retractor muscle to the floor of the lung (character 6, states B, C) and elongation of the vagina (character 18, states B, C) are homoplastic. Obsolescence of radial ribs on the penult and body whorls distinguishes HYB from SPO. In conjunction with increased size, it is a noteworthy convergence upon VAN and occurs in the same region — the moist forests of the Pacific Northwest — where other cases of gigantism in land mollusks are known.

Chromosome number, although known for only two species of the Haplotrematinae and, therefore, not entered in the compatibility analysis, supports the distinction between Ancotrema and Haplotrema. The haploid chromosome number of VAN is 30, that of SPO, 29 (Burch, 1965). The higher number is considered to be apomorphous.

Four characters, all having to do with the reproductive system, distinguish (MIN,VAN) from ((TRA,ALA),(KEE,(DUR, (CON,CAE)))). (MIN,VAN) is defined by the autapomorphy of a swollen vas deferens (character 8, state B). This group contains the type species of Ancomena (VAN, Haplotrema vancouverense) and is here recognized as a restricted subgenus Ancomena of Haplotrema. The other species included in Ancomena by Baker (1931), TRA, ALA, and KEE, are removed from that subgenus. TRA is distinguished from ALA by the absence of a cusp on the central tooth and by minor quantitative differences in shell sculpture and genitalia.
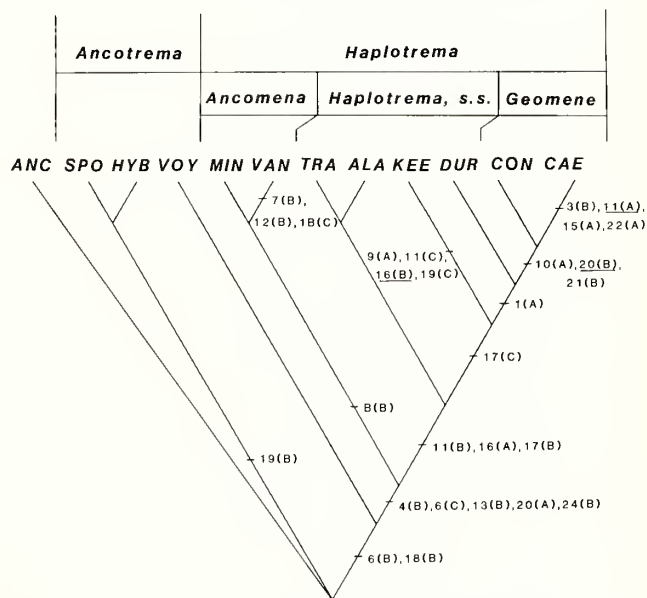

Fig. 3. Phylogenetic hypothesis of the Haplotrematinae, and genus/subgenus boundaries. Underlining denotes reversal; other conventions as in Fig. 1.

The remaining species are a rather heterogeneous lot, although with a clearly hierarchic set of relations. It is easy to see why Baker (1931) and Pilsbry (1946) resorted to three-layered classifications using the infrasubgeneric category "section," but not so easy to decide on a single set of rules for dividing this array into subgenera. (CAE,CON) is holophyletic, with three defining apomorphies. The subgenus name *Geomene*, based on CON, has priority over *Greggiella*, based on CAE. However, four characters distinguish CAE from CON. KEE is holophyletic and distinguished by five characters, including four autapomorphies. My decision has been to recognize no monotypic subgenera and to accept two heterogeneous subgenera (in addition to *Ancomena*) in *Haplotrema* — *Haplotrema, sensu stricto,* and *Geomene.* Table 3 presents a revised classification of the Haplotrematinae based on this analysis.

PLACEMENT OF TAXA NOT ANALYZED

catalinense. Differs from *Haplotrema duranti* principally in larger size (diameter 5.7-6.3 mm versus 5.2 mm). Fine and partly obsolete ribbing occurs also in several mainland populations of *H. d. continentis.* Dissection of both *H. catalinense* and *H. d. duranti* is needed. *Haplotrema s.s.*

costatum. Character of ribbing suggests relationship to *Haplotrema caelatum*, but shell sculpture is not diagnostic in subgenus *Geomene.* Subgenus uncertain.

guadalupense. Differs from *Haplotrema duranti* mainly in absence of ribbing and smooth surface. *Haplotrema s.s.*

kendeighi. Probable sibling species of *Haplotrema con-*

Table 3. Revised classification of the North American Haplotrematidae.

Superfamily Rhytidoidea Pilsbry, 1895
  Family Haplotrematidae Baker, 1925
    Subfamily Haplotrematinae Baker, 1925
      Genus *Haplotrema* Ancey, 1881
        Subgenus *Haplotrema, sensu stricto*
          H. (H.) duranti (Newcomb, 1864)
            H. (H.) d. duranti
            H. (H.) d. continentis Baker, 1931
          H. (H.) catalinense (Hemphill *In:* W. G. Binney, 1890)
          H. (H.) guadalupense Pilsbry, 1927
          H. (H.) keepi (Hemphill, 1890)
          H. (H.) alameda Pilsbry, 1930
          H. (H.) transfuga (Hemphill *In:* W. G. Binney, 1890)
        Subgenus *Geomene* Pilsbry, 1927
          H. (G.) concavum (Say, 1821)
          H. (G.) kendeighi Webb, 1951
          H. (G.) caelatum (Mazÿck, 1886)
        Subgenus *Ancomena* Baker, 1931
          H. (A.) vancouverense (Lea, 1839)
          H. (A.) minimum (Ancey, 1888)
        Subgenus uncertain
          H. costatum Smith, 1957
      Genus *Ancotrema* Baker, 1931
          A. sportella (Gould, 1846)
          A. hybridum (Ancey, 1888)
          A. voyanum (Newcomb, 1865)

cavum. Hubricht (1956) distinguished it from *H. concavum* by the color of the foot and by the large atrium, "at least twice the size of that of [*H. concavum*]," even in smaller animals. None of the reported characters associates *H. kendeighi* with any West Coast species of *Haplotrema. Geomene.*

HISTORY OF THE HAPLOTREMATINAE

Chambers (1987) calculated the average chromosomal rate of evolution for land pulmonates at 0.021 karyotypic changes per lineage per million yr. This figure is derived from the fossil record of land snail genera (Chambers, 1987), which (a) represents *minimum* maximum ages and (b) is far more fragmentary than that of marine genera. The "short-weighting" that results from these features is somewhat counterbalanced by the tendency for paleontological systematics — based, necessarily, on shell characters alone — to construe genera broadly and by the frequency of convergence in pulmonate shell form.

After excluding *Haplotrema* (=*Ancotrema* + *Haplotrema* of this study) from Chambers's data set to avoid circularity, and recalculating the rate of karyotypic changes based on a recent Cenozoic time scale (Berggren *et al.*, 1985), using mean rather than maximum ages for the fossils of an epoch or sub-epoch, the data suggest an approximate age of 42.5 million yr (late middle Eocene) for the Haplotrematinae. It must be stressed that this estimate is based solely on an average derived from a wide variety of land pulmonates.

Fossil evidence indicates that during the middle Eocene a diverse land mollusk fauna including genera of present-day tropical distribution existed at middle latitudes in North America (Roth, 1984, 1988; Roth and Megaw, 1989). By the late middle Eocene many of these genera had begun to retreat southward and a latitudinal stratification of land mollusk faunas had become evident. The dichotomy between the temperate Haplotrematinae and its tropical out-group, the Austroselenitinae, could have arisen at this time.

The phylogenetic hypothesis indicates an early dichotomy between *Ancotrema* and *Haplotrema*, with the species of *Ancotrema* retaining more characteristics of the hypothetical ancestor. Other trends include: (a) a tendency toward reduction of vaginal musculature as one moves toward the right side of the cladogram in figure 3; (b) a parallel tendency toward greater penial complexity; (c) migration of the origin of the penial retractor muscles from the columellar muscle bundle to floor of lung (presumably increasing mechanical efficiency); (d) parallel instances of gigantism in the Pacific Northwest; (e) size reduction southward along the Pacific Coast (partly, but not wholly, on islands) correlating with the presence/severity of a summer dry season; (f) a homoplastic continuation of the loss or reduction of cusps on the teeth of the radula.

The dichotomy between the widespread eastern North American species, *Haplotrema concavum*, and a West Coast species (the highly derived *H. caelatum*) occurs higher on the tree (i.e. later in time) than the origins of all other major West Coast lineages. The vicariance was probably not related to the Laramide orogeny (which would require condensing most

of haplotrematine evolutionary history into the later Eocene) but to a later climatic event, such as the late Tertiary emergence of an arid environment in the American Southwest (Axelrod, 1979) or Pleistocene glacio-pluvial changes, which were relatively mild in coastal southern California (Johnson, 1977) but profound in the continental interior. Several other characteristically "eastern" taxa such as the genera *Stenotrema* Rafinesque, 1819 (Polygyridae), and *Hendersonia* Wagner, 1905 (Helicinidae), were present in the North American cordillera as recently as early (and possibly middle) Miocene time (Berry, 1953; Roth and Emberton, unpub. data), but the timing of their extinction in the cordillera is uncertain.

LECTOTYPE DESIGNATION FOR *SELENITES VANCOUVERENIS* FORMA *HYBRIDA* ANCEY, 1888

Three localities were cited in the original publication of *Selenites vancouverensis* forma *hybrida* Ancey, 1888: "Oregon, dans la region du Fleuve Columbia; Portland, Oregon (Dore); territoire de Washington." Type material was not specified. Baker (1931) designated Portland as the type locality. C. F. Ancey's collection was dispersed by the shell dealer Geret (Dance, 1966). One syntype, purchased from Geret by S. Stillman Berry in the early years of this century, is now in the Santa Barbara Museum of Natural History. On a printed label of "Geret, Conchyliologiste/Naturaliste" an unknown hand gives the locality as Astoria, Oregon. A second hand has written in pencil, "TYPE". The specimen is a mature shell, 24.2 mm in maximum diameter, 11.0 mm in height, with 6.2 whorls, agreeing with the original description but slightly lower-spired than Ancey's figure. The specimen, SBMNH 35134 (Fig. 4), is here designated lectotype of *Selenites vancouverensis* forma *hybrida*. The type locality of the taxon is therefore Astoria, Clatsop County, Oregon, rather than Portland as designated by Baker (1931).

Ancey (1888) stated that he was maintaining the name "hybrida" under which J. H. Thompson had designated the taxon in his private collection. The name seems to have had even wider currency among amateur malacologists of the time. Hemphill (1890a) listed "*Selenites concava* var. *hybrida*" in a sales catalog and, apparently unaware of Ancey's (1888) proposal, described the same taxon as *Selenites van-*

couverensis var. *hybrida* (Hemphill, 1890b), likewise based on specimens from Astoria (Coan and Roth, 1987).

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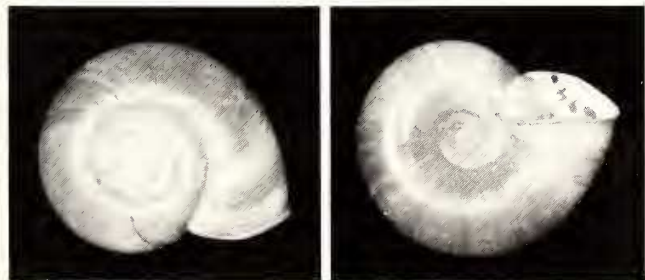

Fig. 4. Lectotype of *Selenites vancouverensis* forma *hybrida* Ancey, 1888, SBMNH 35134; top and basal views. Diameter 24.2 mm.

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Note added after revision. One anonymous reviewer of this paper performed a maximum-parsimony analysis (Farris, 1983; Kluge, 1989) of this data set using the program HENNIG86 (Farris, 1988). Four equally (and maximally) parsimonious trees were derived. One tree was isomorphous with the tree shown in figure 3; a second differed in having the branch leading to KEE and that leading to (TRA,ALA) reversed. Two other trees contained the grouping (((MIN,VAN),KEE),((TRA,ALA),(DUR,(CON,CAE)))). A classification based on this additional analysis might include KEE in the subgenus *Ancomena* and treat (TRA,ALA) as a group coordinate in rank with (DUR,(CON,CAE)).

APPENDIX A. LIST OF CHARACTERS, CHARACTER STATES, AND CHARACTER STATE TREES

Character No. 1. Right ocular retractor: in penioviducal angle (A), free from genitalia (B); B → A.

Character No. 2. External genital orifice: close to base of right ommatophore (A), distant from right ommatophore (B); B → A.

Character No. 3. Radula: with several lateral teeth bicuspid (A), with one lateral tooth bicuspid (B); A → B.

Character No. 4. Central tooth of radula: with multiple cusps (A), with reduced number of cusps (0-1) (B); A → B.

Character No. 5. Central tooth: with cusps (A), lacking cusps (B); A → B.

Character No. 6. Penial retractor muscle origin: on left side of columellar muscle (A), on floor of lung with strands from columellar bundle (B), on floor of lung (C); A → B → C.

Character No. 7. Penial retractor muscle insertion: at summit of penis with vas deferens entering laterally (A), on vas deferens, which enters penis apically (B); A → B.

Character No. 8. Vas deferens: slender throughout (A), with swollen, epiphallus-like portion (B); A → B.

Character No. 9. Penis: with flagelloid caecum (A), without (B); B → A.

Character No. 10. Penis: with diverticulum (A), without (B); B → A.

Character No. 11. Penial chamber wall: without papillae (A), with sharp, thornlike papillae (B), with blunt papillae (C); A → B → C.

Character No. 12. Apical penial chamber: well differentiated (A), not well differentiated (B); A → B.

Character No. 13. Principal penial chamber: differentiated into apical and basal parts (A), not differentiated thus (B); A → B.

Character No. 14. Penial sheath: present (A), absent (B); B → A.

Character No. 15. Penial chamber: with apical papilla (A), without (B); B → A.

Character No. 16. Atrium: with "stimulator" (A), without (B); B → A.

Character No. 17. Vagina: with shining muscular collar (A), with sphincteric thickening (although not a muscular collar) (B), without collar or thickening (C); A → B → C.

Character No. 18. Vagina: extremely short (i.e., spermathecal duct origin directly above atrium) (A), somewhat less than to approximately equal to length of penis (B), 1.5 times length of penis (C); A → B → C.

Character No. 19. Base of spermathecal duct: weakly dilated (A), strongly dilated (B), with a dual dilation (C); B ← A → C.

Character No. 20. Length of kidney: 1.5 times its base (A), approximately 2 times its base (B), over 2 times its base (C); C → B → A.

Character No. 21. Length of pericardium: approximately ⅔ length of kidney (A), approximately ½ length of kidney (B); A → B.

Character No. 22. Embryonic shell: with radial riblets on last ½ whorl (A), smooth throughout (B); B → A.

Character No. 23. Shell: with distinct, round-topped radial ribs as broad or broader than interspaces (A), with round-topped radial ribs narrower than interspaces (B); with fine, threadlike to laminar radial ribs (C), without ribs (except for low undulations of shell surface) (D); D ← A → B → C.

Character No. 24. Shell: with coarse spiral striae cutting tops of radial ribbing (A), without (B); A → B.

Character No. 25. Shell: with minute, close, wavy spiral striae (A), without (B); A → B.